

Behavioural traits as an aid to solving taxonomic problems

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Until the end of the last century taxonomists relied entirely on morphological data obtained from skin collections. An article by Whitman (1898) entitled "Animal behavior" was the first publication to appear on this subject and accordingly attracted much attention. Later, the behaviour of the Anatidae was studied by Heinroth (1910), and thereafter, especially from 1927 and 1930 onwards, Lorenz published numerous papers, including (1941) reporting a comparative study of the behavioural patterns of 20 different species of the Anatinae, which considered the behaviour of females, males and young birds separately.

The methods employed in Lorenz's studies on tame ducks living under natural conditions were of a pioneering nature. Thereafter, all behavioural studies were carried out on birds kept under natural conditions, or by observing wild birds from a hide. Subsequently the literature on ethology has been voluminous.

However, in order to derive a taxonomic interpretation from behaviour, it has first to be decided which aspects of behaviour from which functional system are suitable for this purpose. Obviously of little value are behavioural components that are strongly influenced by abiotic and biotic environmental factors (such as climate, temperature, day length, form of vegetation, food supplies etc). Furthermore, we know that certain ecotypes, such as those of aquatic birds and birds of the high mountains, or those living in rocky regions, invariably exhibit convergent specific adaptations to their particular environment. We are, therefore, limited to behavioural traits that are influenced to a minimal degree by the environment, e.g. nest building, brood care, nestling behaviour, and to some extent also social behaviour and certain calls. All aspects of behaviour connected with obtaining food, on the other hand, on account of their high susceptibility to adaptive radiation, should be treated with caution. Nevertheless, certain elements of such behaviour can be extremely informative, such as the use of the foot in manipulating food, or other special adaptations. The greater the number of functional systems for which behavioural differences can be demonstrated, the more informative are these results for our present purpose.

Behavioural comparisons in the Regulidae

The classification of the family Regulidae recommended by Sibley & Ahlquist (1985) was not entirely acceptable. Additional uncertainties arose from a re-evaluation of the genetic differentiation of the American twin species *Regulus satrapa* and *R. calendula* by Ingold *et al.* (1988). On the basis of their investigations the authors claimed that the 2 species are "not closely related", which, as they pointed out, had already been

TABLE 1

Breeding and other behaviour in 4 species of *Regulus* to demonstrate the many differences in *R. calendula*

Goldcrest <i>R. regulus</i>	Firecrest <i>R. ignicapillus</i>	Golden-crowned Kinglet <i>R. satrapa</i>	Ruby-crowned Kinglet <i>R. calendula</i>
Social behaviour			
in migratory and wintering flocks contact sleep	same	same	same no contact sleep
Breeding			
territorial; hanging nest	same	same	same
Nesting material			
very fine	same	same	also stalks and leaves
Courtship			
no courtship feeding	courtship feeding	courtship feeding	no courtship feeding
Nestling nutrition			
mainly collembola, tiny arthropods	soon larger prey	same as <i>ignicapillus</i>	same as <i>ignicapillus</i>
Nestling			
down on head	same	same	no down
Nestling period			
(days): 22	22–24	19–20	18–19
Nestling behaviour			
huddle together after leaving nest; return to nest for 1–2 days	same same	same same	do not huddle after leaving nest; do not return to nest
Territorial song			
typical for Regulidae	same	same	atypical in frequency and phrasing

claimed by Mayr & Short (1970). Assuming that the 2 species reached the American continent at different times, Ingold *et al.* concluded that the "DNA data suggest that the Ruby-crowned Kinglet [*R. calendula*] is the most recent arrival". If, however, the 2 species are judged on the basis of their behaviour, and if they are compared in a similar way with the European twin species *R. regulus* and *R. ignicapillus*, it is impossible to agree with Ingold *et al.*'s conclusion (see Thaler 1988) (Table 1). E. Mayr

(pers. comm. 1988) also expressed his doubts: "surely this Ruby-crowned kinglet arrived in North America long before the Gold-crowned [*R. satrapa*], not the reverse . . .".

The most striking differences in behaviour between *calendula* and the other 3 species are seen, for example, in connection with display (Fig. 1), which, although always species-specific, only in *calendula* differs entirely from the Regulidae pattern (Thaler 1988), as also in its song (see also Mayr 1956). In addition only in *calendula* do some of the first-year males regularly show delayed maturation plumage (i.e. may moult into a second juvenile plumage) (Thaler in press), whereas the other Regulidae species avoid intraspecific aggression in their first year by 'behavioural mimicry' (i.e. concealing the orange in their crown and behaving like females) (Thaler 1979, 1990). The complete absence of nestling down in *calendula* probably further differentiates it from other Regulidae. Thaler (1988) showed that *ignicapillus* has more primitive behavioural patterns than *regulus* and is most probably the common ancestor of all Regulidae. It would seem therefore that *calendula* has evolved from *ignicapillus* and in isolation in America has since acquired the differentiating characteristics which separate it from *satrapa*, the later arrival which has differentiated little as yet.

Behavioural traits of *Leptopoeile sophiae*

Although Severtzov's Tit Warbler *Leptopoeile sophiae* is no unfamiliar species (see Ali & Ripley 1971/2, Dementiev & Gladkov 1954), our knowledge of its behaviour is incomplete and its systematics still await clarification. Nicolai & Wolters (1971) placed *Leptopoeile*, presumably on account of its minute size, among the Regulidae, in whose vicinity it was also placed by Hartert (1916) and Stresemann *et al.* (1937). Schäfer (1938) placed it close to the tits, particularly to the Aegithalidae. The genus was not considered by Sibley & Ahlquist (1985). One of us has kept 4 pairs of *Leptopoeile sophiae* in aviaries since 1990, and it seems that *Leptopoeile* had not previously, at least for any length of time, been kept in aviaries. A wealth of unknown behavioural details was to be expected and was observed. Their social behaviour appeared highly developed and ritualized, and the existence of social courtship behaviour and group 'helpers' can be assumed. *Leptopoeile*, like *Regulus*, feeds on arthropods and, because it inhabits thickets, they also appear to have certain similar foraging strategies, since these are influenced by the environment. Nevertheless, when carefully observed they prove to differ fundamentally in feeding habits. *Leptopoeile* uses its feet (Fig. 2), tending to a similarity with the Aegithalidae (cf. e.g. *Aegithalos concinnus*—Löhr 1985), with which they also share social behaviour and nest-building characteristics (Table 2).

Behavioural comparisons between the Sittidae and Paridae

The nuthatches (Sittidae) and the tits (Paridae) provide good examples of the fact that purely morphological studies do not necessarily yield unequivocal results. Hartert (1910–1922), convinced that these 2 families

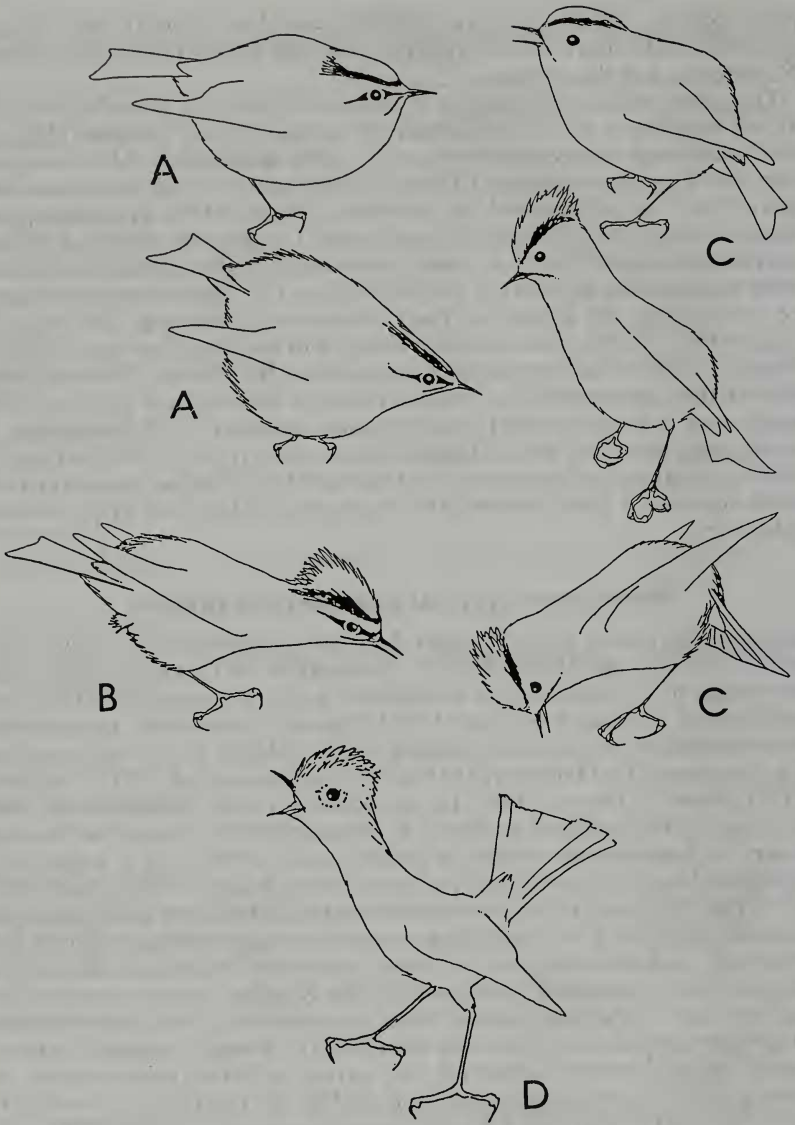


Figure 1. Threatening behaviour of (A) *Regulus ignicapillus*, (B) *R. ignicapillus* and *R. satrapa*, (C) *R. regulus* and (D) *R. calendula*. Adapted from Thaler-Kottek (1986).



Figure 2. Severtzov's Tit Warbler *Leptopoeile sophiae* manipulating a moth by use of the foot.

TABLE 2

Breeding and other behaviour comparisons in *Leptopoeile sophiae*, Regulidae and Aegithalidae

<i>Leptopoeile sophiae</i>	Regulidae	Aegithalidae
Social behaviour		
year-round social or group territoriality ('helpers')	seasonally monogamous	year-round social or group territoriality ('helpers')
Nesting site, type of nest		
in bushes, oven-shaped nests	in trees, bowl-shaped, hanging nests, opening above	in bushes and trees, oven-shaped nests, supported or hanging
Courtship		
no courtship feeding	courtship feeding in <i>ignicapillus</i> and <i>satrapa</i>	no courtship feeding
Food		
arthropods	arthropods	arthropods
Foraging		
uncovers hidden food	eats visible food only	uncovers hidden food
Feeding strategies		
uses feet, even clamps prey; searches ground by scattering litter and turning over leaves	feet never used; prey 'killed' by banging	uses feet; does not search ground
Vocalizations		
clicking, purring	pure, high-pitched notes	clicking, purring

were closely related, placed the Paridae immediately after the Sittidae. A similar view was held by Vaurie (1959), who brought the Paridae even closer to the Sittidae by placing the latter as a subfamily, Sittinae, in the Paridae. However, this sequence was again completely altered on the basis of purely morphological considerations by Wolters (1975–1982), in his principal publication. For him, the Sittidae and Paridae were unrelated and far removed from one another. Between them he placed, for example, the extensive families of Nectariniidae, Estrildidae, Ploceidae and Emberizidae, and even the Sylviidae—as a separate family—are considered before the Paridae.

The distance placed between the nuthatches and tits by Wolters clearly shows that even the most conscientious examination of morphological characteristics of dead animals is, on its own, an inadequate means of arriving at reliable systematic conclusions. Following DNA hybridization studies, Wolters (1983) did in fact modify his views, placing the Sittidae nearer to the Paridae again.

Table 3 gives a comparison of the breeding and feeding habits of tits and nuthatches, based on detailed observations (Löhrl 1958, 1964, 1974, 1991). The behavioural traits cited are partially dependent on breeding site and environment. Inhabitants of tropical and subtropical regions gather no food reserves (e.g. Velvet-fronted Nuthatches *Sitta frontalis* and probably the African tit species). In Europe the Great Tit *Parus major* and the Blue Tit *P. caeruleus* do not lay up stores, but compensate for winter population losses resulting from food shortage by producing large numbers of offspring.

Behavioural traits of *Tichodroma muraria*

The Wallcreeper *Tichodroma muraria* was formerly grouped with the treecreepers (Certhiidae), e.g. by Hellmayr 1903, Hartert 1910–1922, due to false interpretation of their similar bills. Later it was considered as a subfamily of the Sittidae (Vaurie 1959, Peters 1967, Sibley & Ahlquist 1985) or even to be a distinct family (Voous 1977, Wolters 1975–1982).

Behavioural traits can only be taken as evidence of possible affinities if they are not ecological adaptations. In this particular specialist of high mountain regions, however, most of its characteristic movements are adaptations to its habitat. This is also true of its manner of seeking food and its flight. The exceptionally large wings permit the bird to exploit updraft to transport it from the depths of gorges into the upper regions. In searching for a behavioural trait of the Wallcreeper that is with certainty not an adaptation to its habitat, the possibility of a close affinity to the nuthatches was suggested by their similar attitudes in inter- and intra-specific conflicts; both the Wallcreeper and nuthatches adopt the same threatening posture, letting their wings hang and holding their tails erect (Fig. 3). Such a posture is seen in neither tits nor treecreepers. In addition, during the breeding season a gliding form of flight is observed in all nuthatches and also in the Wallcreeper (Löhrl 1988).

On the other hand, other forms of nuthatch behaviour, such as the way they handle food or, with the exception of tropical species, the laying-up of food stores, distinguish nuthatches from the Wallcreeper so clearly that

TABLE 3

Comparison of behavioural traits of tits (Paridae) and nuthatches (Sittidae) (but see text)

Similarities

Breeding behaviour	<p>Nests in holes in trees, the holes enlarged to the required size where necessary. In larger holes the nesting space is partially filled with moss or wood. Cracks in the walls are stopped up with nesting material.</p> <p><i>Nesting material:</i> moss, wool, feathers, pieces of bark.</p> <p>Eggs covered up with nesting material before incubation begins.</p> <p>Incubation of completed clutch can be postponed by as much as a week in periods of bad weather.</p> <p><i>Courtship feeding</i> of female by male during nest-building period.</p> <p>Young fed by both parents.</p> <p><i>Long nestling period:</i> 18–23 days.</p>
Feeding behaviour	<p>Summer: insects and spiders.</p> <p>Winter: spiders, insects and plant diet.</p> <p>Sometimes lay up stores. Hidden food reserves sometimes covered up. Seeds sometimes deposited on a branch before storing.</p>
Other behavioural traits	<p>Wing flicking when excited.</p> <p>Distraction behaviour: droops, waves and spreads wings and tail.</p>

Differences

	Tits	Nuthatches
Breeding behaviour	<p>Incubation 12–15 days.</p> <p>Defends brood by complex defence behaviour: hissing, flapping wings against sides of hole, bill-snapping.</p>	<p>Incubation 15–18 days.</p> <p>Reduces size of entrance to nest with mud, for security.</p>
Feeding behaviour	<p>Breaks up hard food items while gripping with toes.</p>	<p>Breaks up hard food by pushing it into cracks and hammering with bill.</p>

a separate family for *Tichodroma*, which should follow the Sittidae, seems to be ethologically justified.

Behavioural traits of *Siphia strophciata*

The affinities of the small flycatchers, which are common species in Asia, present special problems. In his generic revision of the Muscicapini Vaurie (1953) divided them mainly between the genera *Ficedula*, *Niltava* and *Muscicapa*. Originally, most of them had been placed in the genus *Muscicapa*—a classification still widely adhered to (e.g. by Ali & Ripley 1972, Etchécopar & Hüb 1983). Earlier taxonomic studies of these species, apart from morphological peculiarities or a comparison of habitats, were restricted to the observation that flycatchers “catch insects in the air”, which holds equally for all 77 species treated by Vaurie, while even today,

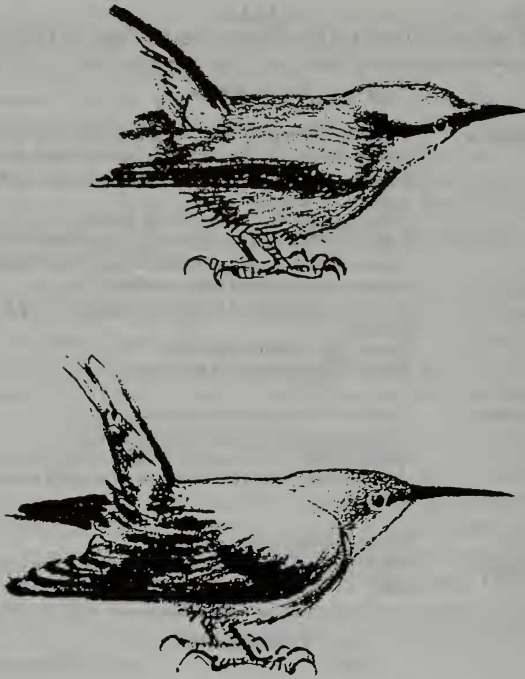


Figure 3. Threatening behaviour of the European Nuthatch *Sitta europaea* (top) and Wallcreeper *Tichodroma muraria* (bottom).

few details of their breeding biology have been described. The accurate observation of differences in behaviour under species-adequate aviary conditions is both possible and rewarding. The Orange-gorgeted Flycatcher *Siphia strophciata* is a good example, as described below.

The systematic position of *S. strophciata* is still controversial: in Hartert (1910–1922) it was termed *Muscicapa strophciata* and Vaurie (1953) considered it “appears to be not too distantly related to the *Ficedula* group”. His decision was made mainly on the basis of morphological characteristics, although he was open to a consideration of such behavioural traits as were available.

Observations on *S. strophciata* kept in cages and aviaries over a considerable number of years revealed a most unusual method of obtaining food, otherwise seen mainly in limicoles (Löhrl 1992). By means of vibrating foot movements the birds shake the twigs on which they are perching and thus mobilise at the surface hidden prey. This is an innate foraging movement, since it was observed not only in several imported mature birds, but also in a young, aviary-hatched, hand-reared individual that had subsequently been isolated and thus had received no ‘instruction’ from an adult. *S. strophciata* is the only species of flycatcher so far known to use this method, and presumably thus secures itself an

advantage over other species. It was not only this unusual method of prey-catching that raised the suspicion that this was not a 'normal' *Muscicapa* or *Ficedula* species. The bird's song resembles rather that of the Bluethroat *Luscinia svecica*, or the Robin *Erithacus rubecula*, and its frequent tail twitching is also seen in the Robin. The impression that its behaviour hardly resembles that of a flycatcher remained unaltered over the 8 years during which one of us observed a number of these birds; no visiting ornithologist thought these birds were a species of flycatcher, and most of them guessed that they were a species of thrush.

The removal of this species from the other flycatcher genera and its renaming (Wolters 1975-1982) as *Siphia strophciata* is fully justified from the ethological point of view.

Discussion

Behavioural patterns can be a useful supplementary help in clarifying some taxonomic questions. It seems that even very advanced techniques such as DNA hybridization are not entirely immune to subjective interpretation or free from errors. Only by considering the bird as a whole are we in a position to ask meaningful questions. Although it may be an exciting idea to take apart such a complex organism and then to attempt to reassemble it as if it were a puzzle, this involves the danger of losing sight of the overall picture, and perhaps also our feeling for the harmony of the whole.

References:

- Ali, S. & Ripley, S. D. 1971, 1972. *Handbook of the Birds of India and Pakistan, together with those of Nepal, Sikkim, Bhutan and Ceylon*. Vols. 6-8. Bombay.
- Dementjev, G. P. & Gladkov, N. A. 1954. *Birds of the Soviet Union*. Vol. 6. Moscow.
- Étchécopar, R. D. & Hüe, F. 1983. *Les Oiseaux de Chine—Passereaux*. Paris.
- Hartert, E. 1910-1922. *Die Vögel der Paläarktischen Fauna*. Berlin.
- Heinroth, O. 1910. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. *Verh. Intern. Ornith. Congr. Berlin*: 615.
- Hellmayr, C. E. 1903. *Das Tierreich 18, Aves: Paridae, Sittidae und Certhiidae*. Berlin.
- Ingold, J. L., Weight, L. A. & Guttman, S. I. 1988. Genetic differentiation between North American Kinglets and comparisons with three allied Passerines. *Auk* 105: 386-390.
- Löhr, H. 1958. Das Verhalten des Kleibers (*Sitta europaea caesia* Wolf). *Z. Tierpsychol.* 15: 191-252.
- 1964. Verhaltensmerkmale der Gattungen *Parus* (Meisen), *Aegithalos* (Schwanzmeisen), *Sitta* (Kleiber), *Tichodroma* (Mauerläufer) und *Certhia* (Baumläufer). *J. Ornith.* 105: 153-181.
- 1974. *Die Tannenmeise*. Neue Brehm-Bücherei 472. Wittenberg-Lutherstadt.
- 1985. Die Rostkappenschwanzmeise (*Aegithalos concinnus*). *Gef. Welt* 109: 334-335.
- 1988. Etho-ökologische Untersuchungen an verschiedenen Kleiberarten (Sittidae). *Bon. Zool. Monogr.* 26: 1-208.
- 1991. Die Haubenmeise, *Parus cristatus*. Neue Brehm-Bücherei 609. Wittenberg-Lutherstadt.
- 1992. *Siphia strophciata*, der Zimtfluckschnäpper. *Tropische Vögel* 13: 3-8.
- Lorenz, K. 1927. Beobachtungen an Dohlen. *J. Ornith.* 75: 511-519.
- 1931. Beiträge zur Ethologie sozialer Corviden. *J. Ornith.* 79: 67-127.
- 1932. Betrachtungen über das Erkennen der arteilgenen Triebhandlungen der Vögel. *J. Ornith.* 80: 50-98.
- 1941. Vergleichende Bewegungsstudien an Anatinen. *J. Ornith. Erg. Bd. III*: 194-293.
- Mayr, E. 1956. *Gesang und Systematik*. Beitr. Vogelkunde 5.
- Mayr, E. & Short, L. L. 1970. *Species Taxa of North American Birds*. Cambridge, Mass. Publ. Nuttall Orn. Club 9.
- Nicolai, J. & Wolters, H. E. 1971. *Vögel in Käfig und Voliere*. Vol. 2. Aachen.
- Peters, J. L. 1967. *Check-list of Birds of the World*. Cambridge, Mass.

- Schäfer, E. 1938. Ornithologische Ergebnisse zweier Forschungsreisen nach Tibet. *J. Ornith.* 86, Sonderheft.
- Sibley, C. G. & Ahlquist, J. E. 1985. The Phylogeny and Classification of the Passerine Birds, based on Comparisons of the Genetic Material DNA. *Acta XVIII. Congr. Int. Orn. Moscow*: 83–121.
- Stresemann, E., Meise, W. & Schönwetter, M. 1937. Aves Beickianae. Beiträge zur Ornithologie von Nordwest-Kansu nach den Forschungen von Walter Beick (+) in den Jahren 1926–1933. *J. Ornith.* 85.
- Thaler, E. 1979. Das Aktionssystem von Winter- und Sommergoldhähnchen (*Regulus regulus*, *R. ignicapillus*) und deren ethologische Differenzierungen. *Bonn. Zool. Monogr.* 12: 1–151.
- 1988. Etho-ökologische Differenzierungen bei amerikanischen Goldhähnchen: *Regulus satrapa*, *Regulus calendula*. *Proc. Int. 100. DO-G Meeting, Current Topics Avian Biol.* Bonn.
- 1990. *Die Goldhähnchen*. Neue Brehm-Bücherei 597. Wittenberg-Lutherstadt.
- Thaler-Kottek, E. 1986. The genus *Regulus* as an example of different survival strategies: adaptation to habitat and etho-ecological differentiation. *Acta XIX Congr. Int. Orn. Ottawa*: 2007–2020.
- Vaurie, C. 1953. A generic revision of flycatchers of the tribe Muscipapini. *Bull. Am. Mus. Nat. Hist.* 100. New York.
- 1959. *The Birds of the Palearctic Fauna. Passeriformes*. Witherby: London.
- Voous, K. H. 1977. *List of Recent Holarctic Bird Species*. British Ornithologists' Union, London.
- Whitman, C. O. 1898. *Animal Behavior*. Biol. Lect. Mar. Biol. Lab. Wood's Hole 285.
- Wolters, H. E. 1975–1982. *Die Vogelarten der Erde*. Berlin.
- 1983. *Die Vögel Europas im System der Vögel*. Baden-Baden.

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